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THE "NICHE-VARIATION" HYPOTHESIS:
A TEST AND ALTERNATIVES

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INTRODUCTION

Often a theory gains acceptance almost for no other reason than its inherent plausibility, the case in point being what has been called the "niche-variation model" (Van Valen 1965). This is the hypothesis that certain kinds of genetic variation and variation of morphological characters, such as bill size in birds, are correlated with and to some extent determined by the variety of foods and habitats used by a population. In its broadest form the hypothesis seeks to explain why some bird species on some islands have greater bill-size variation than on continents (Van Valen 1965; Grant 1967), and why some "central" populations of *Drosophila* are more polymorphic for chromosomal inversions than some peripheral populations (da Cunha and Dobzhansky 1954; da Cunha et al. 1959). In such discussions a term like "niche width" is usually employed, and it is argued that populations in wider niches are more variable than populations in narrower niches, and that the greater morphological variation of the former type of population is the evolutionary expression of the increased fitness of the extreme individuals. For example, the smallest and largest individuals in a population of birds colonizing a species-poor island might choose food items which are relatively small and relatively large, respectively. In the absence of competing species and in the presence of a uniform distribution of food-item size, these extreme individuals would prosper compared to the more abundant typical individuals. The resulting reproductive advantage of the extreme individuals will lead to an evolutionary increase in the variance of bill size. The argument so stated seems reasonable, other things being equal. Essentially the same argument is often couched in less specific terms, namely that there will be "less selection" (a relaxation of stabilizing selection) in a relatively commodious environment. When phrased in this more neutral fashion, the argument is, if anything, less controversial, but it still assumes a *relative* increase in the reproductive success of extreme individuals. On the other hand, if diet-item diversity and variation are uncorrelated, a model invoking intrapopulation feeding specialization in "euryphagous" species is unsupported.

A good theory should be testable and should generate verifiable predictions. For instance, one would expect to find a correlation of bill size and

food-item size within a population under natural and experimental conditions. Besides such behavioral predictions there are also evolutionary tests. This is an attempt at the latter type of verification.

We reasoned as follows. If resource subdivision can be the basis for reduction of intraspecific or intrapopulation competition, and if diversity in type or size of food item is such a resource variable, then such a subdivision should be most clearly expressed in animals with especially varied diets. More particularly, if bill-size differences within a species is a potential means of food apportionment, then putatively "euryphagous" species, like crows, should have more variable bills than putatively "stenophagic" birds like flycatchers.

MATERIALS AND METHODS

The material consists of six species of Central African birds from Malawi (formerly Nyasaland) and Zambia (formerly Northern Rhodesia). Three of these species, Group I, were chosen because they eat a wide variety of food items. Group I includes *Corvus albus*, the pied crow; *Pycnonotus barbatus*, the blackeyed bulbul; and *Ploceus velatus*, the masked weaver. The pied crow is a large, widely distributed corvid in Africa; there are no described races. They are known to feed on insects, grain crops including maize off the cob, fruit, and carrion; they also prey on eggs, chicks, snails, mice, and the external parasites of game and cattle. The bulbul is an abundant bird in southern Africa, rather similar in habits to the western mockingbird, *Mimus polyglottos*, of North America. It feeds on a wide variety of insects (sometimes hawking for them) and their larvae, fruits, and nectar. There are three subspecies in Zambia based on color differences of the crown feathers (Irwin and Benson 1967). The masked weaver is a common gregarious species in open country. It feeds on grain crops and a variety of fruits, flowers, and insects. There are a number of described races; in Zambia the northern race, *katangae*, is associated with marshes and is replaced in the south by the nominate *velatus* (Irwin, personal communication).

The three species of Group II were chosen because of their relatively restricted diets. They include: *Merops pusillus*, the little bee-eater; *Lagonostica rhodopareia* (*jamesoni*), Jameson's fire finch; and *Serinus sulphuratus*, the bully seed-eater. The bee-eater is uniform in size in Zambia (Irwin, personal communication), although Clancey (1967) has recently described a second, southern race. It obtains its insect food by hawking from low perches in bushes and trees. The fire finch has no described races in Zambia, though a very similar form, *L. rubricata*, is marginally sympatric in some areas (Irwin, personal communication). *Lagonostica* feed on grass seeds almost exclusively even during the nesting season. The bully seed-eater, a common canary, is undistinguished by racial designation. It apparently feeds on buds and a variety of seeds, although enough uncer-

tainty exists about its food habits so that we include it in this group with some reservation.

Except for a series of 14 crows from Blantyre, Malawi, all the specimens are part of the ornithological collection of the National Museum of Rhodesia in Bulawayo. All of the latter specimens were collected in Zambia except for three crows from southern Malawi.

Three measurements were made on all specimens: (1) The depth of the bill on a line passing through the center of the nostrils was measured using a micrometer held in place by a clamp; (2) the length of the bill along the midline of the lower mandible from the tip to the symphysis was measured using a vernier caliper; (3) the length of the flattened right wing from the wrist to the end of the longest primary was measured using a millimeter rule. Measurement error was estimated by taking a second series of measurements on some birds. Error was 1.4% for wing length, 1.6% for beak depth, and 1.4% for beak length. Birds which were obviously immature were not measured.

TABLE 1
BEAK DEPTH

Species and Subsample	<i>N</i>	\bar{x}	<i>S</i>	<i>V</i>	<i>V</i> ²
<i>Corvus albus</i> :					
All specimens	39	19.69	0.88	4.47	20.01
All specimens minus Blantyre	25	19.59	0.98	5.02	25.24
All males	19	19.76	1.01	5.10	26.00
Blantyre	14	19.88	0.61	3.08	9.48
All females	5	18.80	0.40	2.16	4.65
<i>Pycnonotus barbatus</i> :					
All specimens	52	5.32	0.26	4.96	24.65
All males	22	5.45	0.21	3.81	14.52
All females	30	5.22	0.26	5.02	25.19
Females Mwekera	10	5.37	0.26	4.94	24.41
<i>Ploceus velatus</i> :					
All specimens	52	7.28	0.63	8.65	74.87
All males	37	7.56	0.48	6.37	40.52
All females	15	6.57	0.31	4.76	22.66
North males	16	7.14	0.28	3.88	15.02
North females	14	6.55	0.31	4.81	23.10
South and east males	20	7.85	0.31	4.00	15.98
<i>Merops pusillus</i> :					
All specimens	46	4.56	0.24	5.18	26.83
All males	26	4.58	0.22	4.76	22.63
All females	20	4.52	0.25	5.58	31.11
All south	20	4.59	0.24	5.28	27.88
<i>Serinus sulphuratus</i> :					
All specimens	31	8.20	0.37	4.48	20.06
All males	24	8.25	0.38	4.63	21.42
All females	7	8.04	0.25	3.13	9.79
North males	11	8.26	0.41	5.02	25.18
<i>Lagonostica rhodopareia</i> :					
All specimens	38	5.26	0.19	3.56	12.69
All males	24	5.26	0.21	3.96	15.67
All females	14	5.25	0.14	2.76	7.62
All north	12	5.29	0.15	2.87	8.24

The species samples were each subdivided into sex and geographic subsamples in order to reduce heterogeneity and to study the variation within samples from single localities. Geographic subdivision of the samples depended on the nature of each collection. See tables 1, 2, and 3 for the statistics.

For *Corvus* the 14 unsexed specimens from Blantyre were from one flock and constitute a subsample. Fifteen specimens (10 females and five males) of *Pycnonotus* were all collected in the vicinity of Mwekera and are considered separately. The same applies to the 12 specimens of *Lagonostica*, all of which were collected at Kasama. The two geographic subsamples of *Ploceus* correspond to the two races, *katangae* in the northeast from the Bangweulu region north to Tanzania, and *velatus* in the south and southeast. The 20 specimens of *Merops* were all collected in a relatively small area near Kariba—between 17° and 15° south latitude and between 26° and 29° east longitude. The 11 male specimens of *Serinus* were all collected north of 12° south latitude.

TABLE 2
BEAK LENGTH

Species and Subsample	<i>N</i>	\bar{x}	<i>S</i>	<i>V</i>	<i>V</i> ²
<i>Corvus albus</i> :					
All specimens	38	28.82	1.58	5.49	30.10
All specimens minus Blantyre	25	28.91	1.65	5.70	32.49
All males	19	29.10	1.76	6.05	36.65
Blantyre	13	28.65	1.43	4.98	24.83
All females	5	27.94	0.65	2.31	5.36
<i>Pycnonotus barbatus</i> :					
All specimens	52	9.26	0.48	5.16	26.59
All males	22	9.30	0.51	5.45	29.73
All females	30	9.23	0.45	4.89	23.95
Females Mwekera	15	9.14	0.41	4.48	20.07
<i>Ploceus velatus</i> :					
All specimens	52	9.37	0.65	6.92	47.82
All males	37	9.64	0.51	5.31	28.18
All females	15	8.71	0.43	4.95	24.50
North males	17	9.50	0.61	6.40	40.98
North females	14	8.73	0.44	5.02	25.17
South and east males	20	9.76	0.37	3.82	14.61
<i>Merops pusillus</i> :					
All specimens	45	2.16	0.19	8.90	79.25
All males	25	2.19	0.21	9.48	89.88
All females	20	2.13	0.16	7.65	58.53
All south	20	2.28	0.15	6.76	45.74
<i>Serinus sulphuratus</i> :					
All specimens	31	8.54	0.60	7.04	49.52
All males	24	8.57	0.66	7.69	59.06
All females	7	8.44	0.31	3.65	13.31
North males	11	8.57	0.53	6.20	38.44
<i>Lagonostica rhodopareia</i> :					
All specimens	38	6.23	0.45	7.31	53.41
All males	24	6.24	0.47	7.60	57.77
All females	14	6.22	0.42	6.72	45.18
All north	12	5.96	0.29	4.88	23.79

TABLE 3
WING LENGTH

Species and Subsample	<i>N</i>	\bar{x}	<i>S</i>	<i>V</i>	<i>V</i> ²
<i>Corvus albus</i> :					
All specimens	39	34.76	1.89	5.43	29.47
All specimens minus Blantyre	25	35.34	1.77	5.01	25.14
All males	19	35.58	1.90	5.33	28.40
Blantyre	14	33.72	1.62	4.80	23.03
All females	5	34.40	0.97	2.82	7.94
<i>Pycnonotus barbatus</i> :					
All specimens	51	9.52	0.33	3.44	11.83
All males	22	9.66	0.27	2.76	7.62
All females	29	9.41	0.33	3.48	12.12
Females Mwekera	10	9.69	0.33	3.41	11.60
<i>Ploceus velatus</i> :					
All specimens	52	7.04	0.57	8.06	65.04
All males	37	7.30	0.44	6.10	37.15
All females	15	6.41	0.25	3.99	15.95
North males	17	6.88	0.19	2.79	7.80
North females	14	6.41	0.26	4.11	16.89
South and east males	20	7.65	0.23	3.05	9.30
<i>Merops pusillus</i> :					
All specimens	45	8.07	0.23	2.92	8.52
All males	25	8.08	0.20	2.49	6.18
All females	20	8.07	0.27	3.34	11.18
All south	20	8.22	0.20	2.43	5.89
<i>Serinus sulphuratus</i> :					
All specimens	31	7.82	0.21	2.71	7.36
All males	24	7.85	0.20	2.61	6.79
All females	7	7.70	0.19	2.50	6.26
North males	11	7.86	0.20	2.57	6.62
<i>Lagonostica rhodopareia</i> :					
All specimens	38	4.95	0.14	2.87	8.23
All males	24	4.96	0.14	2.84	8.04
All females	14	4.93	0.14	2.84	8.05
All north	12	4.98	0.12	2.46	6.07

For each species sample and its component subsamples the mean, standard deviation, coefficient of variation (*V*) were calculated. The statistic *V*² is employed for comparisons of variation among the species because it is distributed analogously to the variance of a normal distribution so that ratios of *V*²'s are analogous to the *F* statistic (Lewontin 1966) and can be so treated.

RESULTS

Significant sexual dimorphism (table 4) occurs in *Corvus* for bill depth, in *Pycnonotus* for bill depth and wing length, in *Ploceus* for all three characters, in *Merops* for bill length, and in *Serinus* for wing length. It is noteworthy that sexual dimorphism in bill depth occurs in all Group I species and none of the Group II species.

The question arises which of the four to six coefficients of variation (*V*'s) obtained by subdividing the species samples are the best estimates for comparative purposes. We can obviously eliminate the sexually mixed sub-

TABLE 4
t TESTS FOR SEXUAL DIMORPHISM IN SIX SPECIES OF AFRICAN BIRDS

Species and Character	<i>t</i>	df	Probability
<i>Corvus albus</i> :			
Bill depth	2.04	22	0.02 < <i>P</i> < .05
Bill length	1.43	22	0.1 < <i>P</i> < .2
Wing length	1.33	22	0.1 < <i>P</i> < .2
<i>Pycnonotus barbatus</i> :			
Bill depth	3.32	50	0.001 < <i>P</i> < .01
Bill length	0.52	50	0.6 < <i>P</i> < .7
Wing length	2.90	49	0.001 < <i>P</i> < .01
<i>Ploceus velatus</i> :			
Bill depth	7.37	50	<i>P</i> < .001
Bill length	6.25	50	<i>P</i> < .001
Wing length	7.26	50	<i>P</i> < .001
<i>Merops pusillus</i> :			
Bill depth	0.93	44	0.3 < <i>P</i> < .4
Bill length	1.96	43	0.05 < <i>P</i> < .1
Wing length	0.01	43	0.9 < <i>P</i>
<i>Serinus sulphuratus</i> :			
Bill depth	1.34	29	0.1 < <i>P</i> < .2
Bill length	0.51	29	0.6 < <i>P</i> < .7
Wing length	1.78	29	0.05 < <i>P</i> < .1
<i>Lagonostica rhodopareia</i> :			
Bill depth	0.19	36	0.8 < <i>P</i> < .9
Bill length	0.10	36	0.9 < <i>P</i>
Wing length	0.57	36	0.5 < <i>P</i> < .6

samples where significant sexual dimorphism is found. Further, subsamples with 10 or less records are probably not very reliable. This still leaves two to five *V*'s, depending on the species and character. These remaining *V*'s for a character are usually not significantly different from each other, so I have used the lowest of these for comparison. These are indicated by bold face in tables 1, 2, and 3. Wing-length statistics are reported for their comparative value, but are not discussed.

Bill depth (table 1) is considered the most relevant character, since it is probably affected less by growth and differential wear than is bill length (Davis 1954). The *F* tests of the *V*² ratios for bill depth show that the female sample of *Lagonostica* is significantly (*P* > .05) less variable than *Merops* and *Serinus*, and that the Blantyre sample of *Corvus* is significantly less variable than *Merops*, the latter in spite of the sexually heterogeneous nature of the Blantyre sample.

If the bill-length statistics are taken at face value, *Merops* and *Serinus* are significantly more variable than *Ploceus*. Otherwise, there are no significant differences in bill variation.

CONCLUSIONS AND DISCUSSION

Our interpretation concerning the levels of bill variation in the six species is that birds with a broad range of food items appear to be no more variable than birds with less eclectic diets. In tables 5 and 6 are presented

TABLE 5
BILL VARIATION IN SOME BIRDS THAT EAT MANY DIFFERENT FOODS

SPECIES AND LOCALITY	SEX	DEPTH		LENGTH		SOURCE
		N	\bar{x}	N	\bar{x}	
Skua:						
<i>Catharacta skua hamiltoni</i>	M & F	115	22.24	115	63.84	Swales 1965
Parasitic jaeger:						
<i>Stercorarius parasiticus</i>	M	22	28.30	2.7
	F	16	27.78	2.7
Herring gull:						
<i>Larus argentatus smithsonianus</i> . . .	M	55	19.48	55	58.15	4.51
	F	57	17.07	57	51.44	4.23
Glaucous gull:						
<i>Larus h. hyperboreus</i>	M	49	25.77	49	63.17	1.83
	F	56	20.71	56	57.31	3.33
Scrub jay:						
<i>Aphelocoma coerulescens obscura</i> .	M	50	8.57	51	18.98	5.75
	F	25	8.10	27	17.75	5.68
<i>A. c. insularis</i>	M	43	10.61	45	23.51	4.08
	F	35	10.12	37	21.99	4.00
Common crow:						
<i>Corvus brachyrhynchos</i>	M	40	37.3	4.0
	F	47	34.3	1.7
	M	34	39.1	5.0
	F	46	36.5	4.6
Cuban crow:						
<i>Corvus nasicus</i>	M	36	42.2	4.5
	F	24	40.8	4.6

TABLE 6
BILL VARIATION IN SOME BIRDS THAT APPEAR TO BE RELATIVELY SPECIALIZED FEEDERS

SPECIES AND LOCALITY	SEX	DEPTH		LENGTH		SOURCE
		N	\bar{x}	N	\bar{x}	
Pacific loon: <i>Gavia archica pacifica</i>	M	16	48.65	4.2 * Manning et al. 1956
Alaska, Western Canadian Arctic						
Socorro petrel: <i>Oceanodroma leucorhoa</i>	M	41	7.3	42	13.8	5.9 Original*
Guadalupe Island	F	29	7.2	31	13.9	4.3
Arctic tern: <i>Sterna paradisaea</i>	M	32	32.82	5.2 Manning et al. 1956
Eastern Canada and Greenland						
Common murre: <i>Uria aalge</i>	M	65	13.96	117	49.23	4.16 Storer 1952
California	M	19	13.93	24	46.52	3.44 Storer 1952
Northern Alaska						
Hammond's flycatcher: <i>Empidonax hammondi</i>	M	40	3.18	46	7.21	4.38 Johnston 1966
N. California and S. Oregon	F	20	3.12	22	6.99	4.88
Wren: <i>Campylorhynchus griseus</i>	M	50	5.46	47	19.56	4.82 Selander 1964
Vicinity of Tonolá, Chiapas, Mexico	F	53	5.00	53	18.31	3.72
Red crossbill: <i>Loxia curvirostra benderei</i>	M	42	12.4
Oregon	F	19	12.6
...	M	38	11.1
Oregon	F	24	10.7
<i>L. c. sitkensis</i>						Original*
...						Original*

* Specimens courtesy of Joseph R. Jehl, San Diego Society of Natural History.

data showing a similar absence of association in other bird species. Many of the papers cited in the tables present more than one set of data for a species. The figures we give represent the largest sample or, if all samples are about the same size, coefficients of variation which are typical. Taken together, the results do not support the theory that there is a correlation between "niche width" and phenotypic variance among species.

A few points are worthy of elaboration. The sample of pied crows from Blantyre undoubtedly contained individuals of both sexes, thus possibly increasing the variance of bill depth (see table 4). Even so, it might be argued that the probable close relationship of these individuals invalidates comparisons between this sample and the geographic samples of the other species. On the other hand, intraspecific competition among members of the same flocks of crows is at a theoretical *maximum*, so that if a mechanism exists to reduce intraspecific competition by increasing phenotypic variation, the effect should be especially evident in the flock. Like many animals, crows are very opportunistic, feeding on what is abundant at any given time. Perhaps it would be more meaningful if we thought less in terms of niche width and more in terms of degrees of opportunism. In the context of this paper this idea is particularly significant, because even individuals in the most opportunistic species tend to eat the same thing at the same time.

Interspecific competition also bears on this question. If sympatric congeners are the likeliest competitors (see Grant 1966, for references), then of the species in this study, *Corvus* and *Pycnonotus* must have the least interspecific competition (and therefore the "widest niches"). The closest relative of *Corvus albus* is a montane species (*C. albicollis*), and the areas of overlap are small. *Pycnonotus barbatus* has no congeners in Zambia. Each of the other four species has from four to eight congeners in the area of study, the exact number depending on the vagaries of generic allocation. So, for these reasons, too, the theory would predict that *Corvus* and *Pycnonotus* would be more variable. Why then, aren't they?

An alternative strategy for the efficient exploitation of a diversity of accessible foods is polymorphism. The three species of Group I are all sexually dimorphic with respect to beak depth, whereas dimorphism is absent in the other birds (table 4). (Sexual dimorphism was not a factor in choosing the six species.) It seems obvious that, unless there is some reason to expect greater sexual (disruptive) selection in Group I species, the evidence from this study is more in keeping with a "niche width"-polymorphism model than the "niche width"-variation model. But, it could be that there is greater sexual selection for dimorphism in the Group I species. As Smith (1966) warns in his elegant analysis of interspecific interactions in gulls, it is exceedingly difficult to distinguish between selection on bills to reduce nutritional competition on the one hand and to optimize identification of potential mates on the other. Both arguments would predict that sexual dimorphism would decrease in the presence of similar species. The same issue is still unresolved with regard to Darwin's finches (Lack 1947; Bowman 1961). But all of this still evades the main issue, namely, what prevents a significant increase in variation *within* a morph or sex?

Canalization and variation.—An important obstacle to our understanding the bases of phenotypic variation is our ignorance of the complex genetics of such characters as bird bills. Darwin's observation (1897) that the bills of domestic pigeons are highly variable when being strongly selected suggests that the bill is a canalized character. In other words, the distribution of bill sizes will rarely express much of the existing genetic variation in the gene pool. It is known that strong directional selection can undermine canalized developmental systems and increase phenotypic variance (Reeve and Robertson 1953; Robertson 1955; Guthrie 1965). Could the higher levels of variation found in some insular populations by Van Valen (1965) be such a response to directional selection? One of us (Soulé 1966, 1967) has earlier pointed out that new colonists to islands typically find themselves in relatively simplified and novel environments—environments where the resultants of the selective vectors for many characters are highly directional. The rapid and extraordinary evolution of island organisms is strong evidence of these directional pressures. Van Valen consciously selected examples in which the insular populations exist in relatively simple environments—"competing" species normally sympatric on the mainland were absent on the islands. His data also show that the bills of the island populations are typically very different in size (usually larger) from those of the continental counterparts. The same applies to the only case of a significantly greater V for birds on the Tres Marías Islands (Grant 1967). It is possible that *such increases in phenotypic variance in complex characters occasionally observed in small isolated populations living in simplified environments is a transient release of variation concomitant with a deterioration of canalization*. If this is true, we would predict that eventually a new adaptive peak will be reached, the selective mode will then become less directional and more stabilizing, and canalization of the character will again increase and cause a decline in variation. Such a course of events is not necessarily tied to a canalization model. Even traditional population genetics can account for a transient increase in phenotypic variance when a rare genotype has a selective advantage (Warburton 1967). (There are at least two other possible explanations of Van Valen's results: occasional genetic input from the mainland subspecies; the lumping of specimens from geographically differentiated populations on the islands.)

The above hypothesis and the niche-variation model are obviously not mutually exclusive. Yet, if the niche-variation model does account for all or even part of the increase in variation in some insular bird populations, and if such a response had adaptive significance, why then has the effect not been observed in the many very old and well-established insular species that at least potentially have extraordinarily "wide niches"? One example is the Cocos Island representative of the Geospizinae, *Pinaroloxias*. Lack (1945) in his statistical treatment of these birds showed that the variation in bill depth in *Pinaroloxias* is no greater than that of *Certhidea olivacea*, a similar species on a number of islands in the Galápagos archipelago. Yet, *Pinaroloxias* is relatively competitor free. Why hasn't *Pinaroloxias* become

more variable so to better exploit its potentially "wider niche"? We cannot say for certain, but the apparent absence of such a phenomenon in old and stable populations suggests the following rule: Within a single morph (e.g., sex) the variation of complex (involving the integrated development of many organs and tissues) characters is ultimately controlled by selection for a *single* optimum even though this optimum may be a compromise. A corollary of this is that the challenge of disruptive selection, when faced at all by a natural population, is met by either one of two viable responses: (1) The gene pool undergoes total or partial (speciation or polymorphism) compartmentalization, or (2) a narrow compromise mode is selected for, to the exclusion of the two or more potential competing modes.

Certain genetic and epigenetic implications follow. Many of the genes controlling complex characters have pleiotropic effects on other relatively far removed characters. Even if selection is disruptive or destabilizing for such a complex character, stabilizing selection acting on other characters that overlap its genetic and epigenetic base will limit its variability. In principle this idea is testable. It follows that *the fewer the genes influencing a character, or the fewer it has in common with other characters, the less restraint there will be on its variation*. Lerner (1954) has expressed a related set of ideas.

One last point. In this paper, for instance, it would be conventional to use the term "broad food niche" as an equivalent to "feeding on plant and animal material." Yet from a bird's viewpoint, a caterpillar and a berry may be closer together on some hypothetical food axis than a seed and a berry, that is, the hardness may be a more important criterion than the chemistry or the phylogeny. It is logically impossible to avoid this sort of anthropocentric bias. This is not to say that the niche width idea is demonstrably incorrect—it is just that it induces a false sense of security and information content about statements employing the term. An example of this arose in our own study when we found it exceedingly difficult to find species with a "narrow food niche" (see table 6).

SUMMARY

1. It is highly anthropocentric to speak of the width of ecological niches. This and other reasons militate against the utility of the idea.
2. There seems to be no correlation in birds between the variety of foods taken and the variation of bill characters. Hence, the "niche width-variation model" is rejected for complex characters.
3. One or more of the following is likely to cause unusually high variability of a canalized character in a morph of a stable population: (*a*) immigration from genetically different populations, (*b*) directional selection affecting the exposure of theretofore hidden genetic variation, (*c*) mixing individuals from different localities (artifactual variation).
4. It is suggested that a permanent high level of variation in a complex character, even if "adaptive," is improbable because other characters over-

lap its genetic and epigenetic base and stabilizing selection on these related characters will set limits on its flexibility.

5. It follows from (4) that the fewer the genes influencing a character, or the fewer it shares with other characters, the greater its freedom to vary.

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